

EVOLUTION OF *PEROMYSCUS* ON NORTHERN ISLANDS IN THE GULF OF CALIFORNIA, MEXICO.

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ABSTRACT.—Mice of the genus *Peromyscus* on northern islands of the Gulf of California and adjacent mainland areas were examined to trace the divergence of populations there. A total of 27 qualitative characters of the osteology, pelage, phallic morphology, soft anatomy, serology, and karyology was examined in detail. Morphometric characters and dental patterns also were studied, and matings of pertinent forms were attempted with limited success.

The island and mainland forms were treated numerically according to the above qualitative characters, as follows: (1) Two Prim Networks were computed, utilizing different combinations of characters. Each indicated that *P. stephani* (Isla San Esteban) is closely related to *P. boylei*, and that those two species and *P. crinitus* are only distantly related to the remainder of the island and mainland forms. (2) A dendrogram (Wagner Diagram) was computed for the latter, using the quantitative phyletic method. *P. eremicus* was considered ancestral on morphologic and zoogeographic grounds. *P. guardia* (Islas Angel de la Guarda, Granito, and Mejía) is the most divergent of the *eremicus*-like forms and cladistically is closest to *P. merriami*. *P. interparietalis* (Islas San Lorenzo Sur, San Lorenzo Norte, and Salsipuedes) also is relatively far removed from the hypothetical *eremicus*-like ancestor. Populations from the Baja Californian and Sonoran mainlands and Isla Tiburon (*P. eremicus*), and Isla Turner (*P. collatus*), are closely related and should be considered conspecific. On zoogeographic grounds, the populations on western Gulf islands (*guardia*, *interparietalis*) probably are derived from a Baja Californian *eremicus*-like progenitor, whereas eastern island forms (*collatus*, *eremicus tiburonensis*) and *stephani* probably are derived from Sonoran *eremicus*-like and *boylei*-like forms, respectively. Evidence from morphology, amount of gene flow between islands and between islands and the mainland, and time of formation of the islands, suggests that the time interval since initial formation of the islands has been the principal factor affecting divergence of the island populations.

Trends in the evolution of certain characters among Gulf *Peromyscus* suggest that complex features may result from simple conditions in the phallus and dentition, and that acrocentric chromosomes derive from a bi-armed condition. The data suggest that the subgenus *Haplomyomys*, which consists of *eremicus*-like species, contains primitive members of the genus.

RESUMEN.—Se estudiaron los ratones del género *Peromyscus* en las islas septentrionales del Golfo de California y zonas adyacentes del continente, con objeto de determinar las divergencias que presentan sus poblaciones. Se examinaron con todo detalle un total de 27 caracteres morfológicos, relacionados con la osteología, pelaje, órganos sexuales externos y otros caracteres anatómicos, serológicos y citológicos. También se analizaron los caracteres morfométricos y la dentición, intentándose además cruces entre las formas pertinentes, obteniendo éxitos muy limitados.

Las formas encontradas en las islas del Golfo de California y en el continente se analizaron numéricamente en cuanto a los caracteres morfológicos arriba mencionados, en la forma siguiente: 1) Se efectuaron dos "Prim Networks," utilizando diferentes combinaciones de caracteres. En cada caso resultó que *P. stephani* (isla de San Esteban) aparecía como pariente próximo de *P. boylei*, y estas dos especies con *P. crinitus* resultan parientes lejanos de las formas restantes que habitan estas islas y el continente. 2) El diagrama dendrítico (diagrama de Wagner) se computó para *P. crinitus*, utilizando el método filogenético cuantitativo. *P. eremicus* aparece así como una especie ancestral, basándonos en la morfología y la zoogeografía. *P. guardia* (islas Angel de la Guarda, Granito y Mejía) es la especie que diverge más de las formas del tipo *eremicus*, y la más próxima en la escala a *P. merriami*. *Peromyscus interparietalis* (Islas de San Lorenzo Sur, San Lorenzo Norte y Salsipuedes) aparece como una segregación lejana del ascendiente hipotético tipo *eremicus*. Las poblaciones de *P. eremicus* de las zonas continentales de Baja California, Sonora y de la isla Tiburon, y las de *P. collatus* de la isla Turner aparecen muy

relacionadas entre sí, por lo que podrían considerarse co-específicas. Bajo el punto de vista zoogeográfico, las poblaciones de las islas occidentales del Golfo (*guardia*, *interparietalis*) derivan probablemente de un progenitor tipo *eremicus* de Baja California; mientras que es posible que las formas de las islas orientales (*collatus*, *eremicus*, *tiburoniensis*) y *stephani* procedan respectivamente del tipo *eremicus* y del tipo *boylei*. Las características morfológicas evidencian un flujo importante de genes de unas islas a otras y entre éstas y tierra firme durante el período de formación de dichas islas; lo cual sugiere que el lapso de tiempo transcurrido desde que se inició la formación de esas islas constituye el factor principal responsable de la divergencia encontrada en las poblaciones insulares.

La tendencia o curso en la evolución de ciertos caracteres en los *Peromyscus* del Golfo sugiere que estructuras complejas pueden resultar simplemente de las condiciones de los órganos sexuales externos y la dentición, y que los cromosomas acrocéntricos derivan de una condición bifurcada. Los datos obtenidos indican que el subgénero *Haplomyomys*, que incluye las especies tipo *eremicus*, contiene los miembros primitivos del género.

The ecologic and geographic characteristics of islands make them particularly suited for studies concerning differentiation and adaptation in natural populations. In general, climatic stability, decreased ecologic diversity, and increased isolation distinguish islands from mainland areas. In the sense of Preston (1962), the plant and animal populations of an island form a complete ("canonical") system as a result of these peculiarities, while mainland populations represent only a "sample" of a more widely distributed and more diverse biota. Thus, effects of isolation are more pronounced on islands than on continental areas.

In addition, islands presumably are subject to colonization by organisms undergoing primary radiation on continental areas. This seems like a reasonable assumption, although the reverse situation undoubtedly occurs to a lesser degree. Consequently, insular populations may constitute unique control groups in which to examine patterns of evolution and divergence of particular groups of organisms.

Mice of the genus *Peromyscus* are widely distributed in North America in insular and mainland situations. They are nearly ubiquitous on island and mainland areas in and surrounding the Gulf of California. No less than 18 species of two subgenera are recognized there, of which ten are island endemics. It appears that at least five of the seven non-endemic species were important for radiation of the group onto the islands of the Gulf. The following account is an assessment of the morphologic, serologic, and karyologic divergence of the island populations of *Peromyscus* relative to one another and to those on the mainland of Baja California to the west and Sonora, Mexico, to the east.

The geographic area of study consists of the northern group of Gulf islands (Figs. 1 and 2). These islands form an irregular chain from one side of the Gulf to the other, thus affording several possible access routes to and from the mainland. In addition, the chain is separable into deep- and shallow-water islands. The latter group consists of islands (Turner, Tiburon) occupying waters within the 110 meter depth contour, the level to which the sea is thought to have been lowered by eustatic changes during the Pleistocene, whereas the former group (San Esteban, Salsipuedes, the Lorenzos, and Angel de la Guarda and nearby islands) consists of islands that attained their present configuration as long ago as Pliocene (Anderson, 1950). Thus, certain of the islands are chronologically much younger than others by virtue of their relatively recent separation from the mainland.

One would expect a greater degree of morphological and genetic differentiation in peromyscines inhabiting distant and deep-water islands as a result of more effective isolation than in those mice on islands in close proximity to the mainland and in shallow water. The latter islands could be subjected to repeated invasions by mice from mainland populations, resulting in suppression of morphological or genetic differences that might

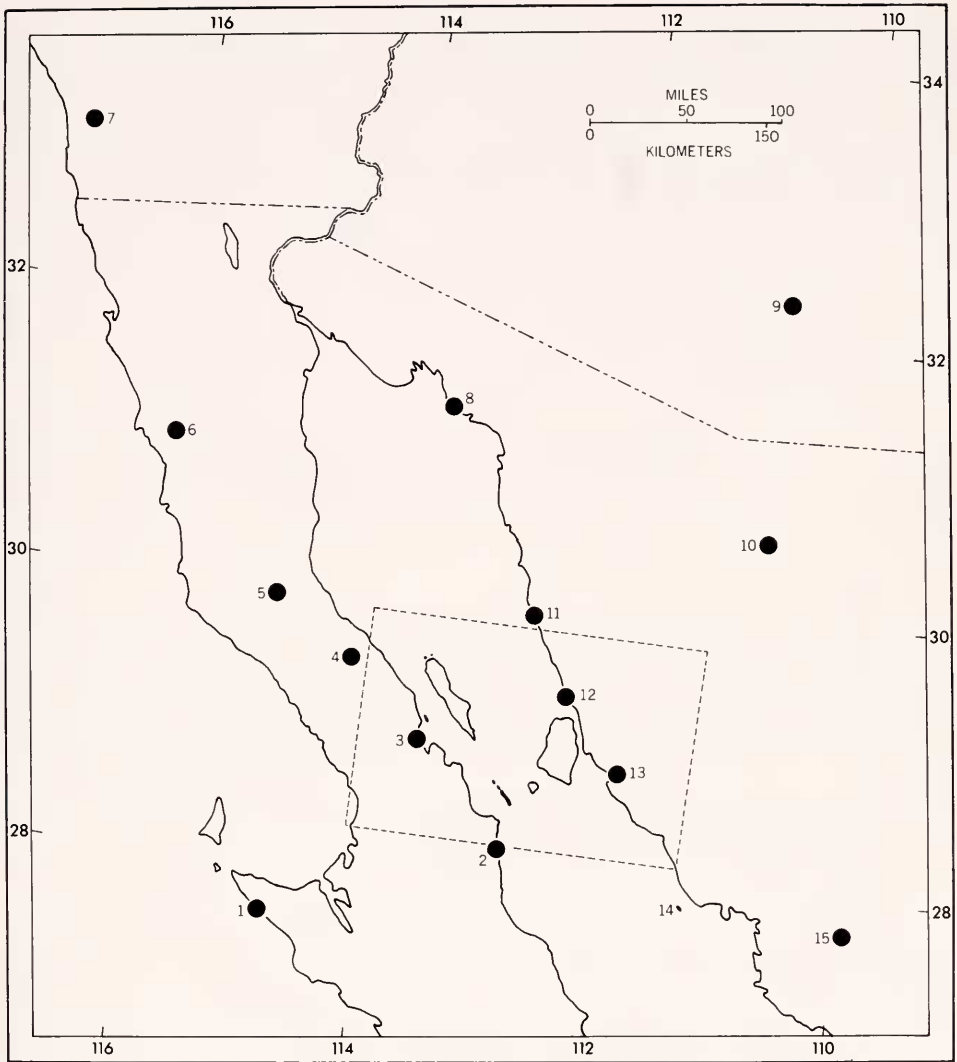


Figure 1. Map of the northern part of the Gulf of California, Mexico, and surrounding areas. The area enclosed in dotted lines is enlarged and presented in detail in Fig. 2. Numbers identify localities discussed in text and specified in "Specimens Examined," and are as follows: 1 — Turtle Bay; 2 — Barril; 3 — Bahía de los Angeles; 4 — San Francisquito; 5 — El Marmol; 6 — San Telmo; 7 — Escondido; 8 — Punta Peñasco; 9 — Tucson; 10 — Imuris; 11 — Puerto Libertad; 12 — Punta Sargento; 13 — Bahía Kino; 14 — Isla San Pedro Nolasco; 15 — Presa Obregon.

otherwise have arisen. However, two other alternatives seem plausible: (1) the environment on the proximal, shallow-water islands may more closely resemble that on the mainland, and (2) the time interval since the initial formation of the shallow-water islands may not have been sufficiently long for a large amount of differentiation to have taken place. The amount and trends of variation in the mice from the different islands and the two mainland areas provide sufficient data for determining which of the above factors is relevant.

The affinities of the species of *Peromyscus* on the northern islands have not been



Figure 2. Map of the northern islands of the Gulf of California, Mexico, and adjacent mainland areas enlarged from the insert in Fig. 1.

thoroughly documented. Currently populations of five species are recognized, all of which are included in the subgenus *Haplomylomys* and are considered closely related to *P. eremicus*:

P. eremicus tiburonensis (Mearns, 1897); Isla Tiburon

P. collatus Burt, 1932; Isla Turner (= I. Datil)

P. stephani Townsend, 1912; Isla San Esteban

P. guardia guardia Townsend, 1912; Isla Angel de la Guarda

P. guardia mejiae Burt, 1932; Isla Mejia

P. guardia harbisoni Banks, 1967; Isla Granito

P. interparietalis interparietalis Burt, 1932; Isla San Lorenzo Sur

P. interparietalis lorenzo Banks, 1967; Isla San Lorenzo Norte

P. interparietalis ryckmani Banks, 1967; Isla Salsipuedes

Taxonomically these forms have remained virtually unchanged since their description, except that *tiburonensis* is now considered a subspecies of *eremicus* (Osgood 1909; cf. Mearns, 1897), and *interparietalis* is considered specifically distinct from *guardia* (Banks, 1967; cf. Burt, 1932). Hooper and Musser (1964b) have suggested, on the basis of phallic morphology, that *stephani* may be closely related to species of the subgenus *Peromyscus*.

MATERIALS AND METHODS

Specimens examined in this study were collected during trips to the Gulf of California and surrounding areas in the summers of 1967 and 1968, and in January, 1969, or were borrowed from the following institutions: California Academy of Sciences (CAS); Dickey Collection, University of California, Los Angeles (UCLA); San Diego Natural History Museum (SD); Department of Zoology, University of Arizona (UA); Museum of

Vertebrate Zoology, University of California, Berkeley (UC); Museum of Natural History, University of Kansas (KU); Museum of Zoology, University of Michigan (UMMZ); and the United States National Museum (USNM). Both live and preserved examples of each of the island populations were obtained.

Except for analysis of variation in dental patterns, only adult wild-caught mice were treated for purposes of studying morphologic, serologic, and karyologic features. All age groups were examined in the former, although specimens with excessive tooth wear were omitted. Adult status was determined according to the methods of Lawlor (1964) and Hoffmeister (1951). Briefly, an animal was considered an adult if there was at least moderate wear on the lingual cusps of M^1 and M^2 (the M^3 generally is well worn at this age), and if the specimen was in advanced ("adult") pelage. Specimens examined for serologic and karyologic properties were considered adult after retention in the laboratory for at least two months.

In osteological considerations I dealt with quantitative and qualitative measures of cranial and other skeletal features. Measurements, in millimeters, were taken with dial calipers. Post-cranial features were examined from whole skeletons except that the number of caudal vertebrae was determined from X-rays. The latter technique provides an accurate means of counting vertebrae and avoids potential error in vertebral counts of whole skeletons owing to vagaries of preparation. External characters include field-taken body measurements and pelage features.

Dental patterns were examined according to a modified scheme of the procedure specified by Hooper (1957). Lophs and styles were considered present only if they comprised a prominent element of an enamel valley. Even so, considerable variation accrues in the development and appearance of these structures. Variation is particularly evident in the shape and placement of styles, but no rigorous attempt was made to determine homologies.

Phalli of freshly killed mice were extracted and fixed in 10% formalin. After everting the prepuce over the proximal portion of the glans, the following procedure was used for clearing and staining:

2% KOH solutionca. 60 minutes
Alizaren red stain (in 2% KOH) 1-2 hours
Distilled water wash 1 minute
Solution of 2 pts. HOH, 1 pt. glycerinca. 24 hours
Solution of 1 pt. HOH, 2 pts. glycerinca. 24 hours
Glycerin permanent storage

The procedure for dried specimens differed slightly. Good results were obtained by shortening the clearing and staining times by about one-half. This reduces the chances for sloughing of the epithelial layer, a common occurrence if the glans was kept in KOH solutions for long periods. The remaining steps were the same.

Karyotypes were examined by means of a bone marrow technique (Patton, 1967). An average of 10 metaphase cells was counted to determine the diploid number of each individual. The fundamental number ("Nombre Fundamental" of Matthey, 1951) was determined as the total number of autosomal arms (excluding the sex chromosomes). The system for describing the chromosomes (Patton, 1967) was as follows:

<i>Chromosome type</i>	<i>Arm ratio</i>
Metacentric	Less than 1:1.1
Submetacentric	1:1.1 to 1:1.9
Subtelocentric	1:2 or greater
Acrocentric (telocentric)	One arm only

Electrophoretic analyses were made according to the modified method of Smithies (1955) used by Brown and Welsler (1968).

The taxonomic designations that are applied below to island and mainland populations concerning character diagnoses, and the discussion of phylogenetic and zoogeographic relationships that follows, correspond to the currently held taxonomy of those forms (see above). They are used only to facilitate interpretation by the reader; they do not reflect any taxonomic evaluation made prior to construction of the phylogeny and taxonomic conclusions.

Statistics and construction of the dendrogram and phenograms were calculated by use of an IBM 360/67 computer at the University of Michigan Computation Center.

MORPHOLOGIC VARIATION MORPHOMETRIC CHARACTERS

A total of 20 external and cranial dimensions was examined. Six of these (total length, length of tail, greatest length of skull, zygomatic breadth, length of rostrum, and length of maxillary toothrow) are presented in Figs. 3-5. The remainder are either relatively invariable or exhibit similar geographic changes as the ones treated in detail here.

Mice of the *guardia* islands (Angel de la Guarda, Mejía, and Granito) show no consistent trends of inter-island variation in size, although significant differences ($P < .05$) are evident in certain dimensions. However, *interparietalis* (Isla Salsipuedes, San Lorenzo Norte, and San Lorenzo Sur) exhibits a trend of increasing size in nearly all dimensions from Salsipuedes in the north to San Lorenzo Sur in the south. An exception is zygomatic breadth, and the relative constancy of this dimension together with the variation for greatest length of skull gives *interparietalis* from Salsipuedes a shorter, broader-headed appearance than its southern island counterparts. *P. stephani* (Isla San Esteban) differs from other island forms in having cranial dimensions that usually average larger.

In general, forms from Islas Turner (*collatus*) and Tiburon (*eremicus*) were similar to mainland *eremicus* on the basis of morphometric characters. Other mainland populations of *eremicus* in the Gulf area do not differ importantly from the two samples given in Figs. 3-5 (for example, see Lawlor, in press).

The large differences in certain dimensions evident between insular populations of the same species (e. g., in *interparietalis* and *guardia*) suggest that isolation of these mice on islands has resulted in the retention of morphometric differences that generally are eliminated by higher rates of gene flow in continental populations. For example, differences of significant proportions usually are not evident in morphometric data for mainland populations of *eremicus* (*Ibid.*).

DENTAL PATTERNS

Dental topography in all of the island forms is relatively simple. The enamel valleys between major cusps generally are unobstructed except for styles. The most common accessory tooth structures are ectostylids on the lower molars (M_1 and M_2) and mesostyles on the uppers (Figs. 6, 7; Table 1); the latter are more variable in frequency and are found uncommonly on the second molars. Mesolophs occur at high frequency in the M^1 only in mice from Islas Granito and San Esteban, whereas entolophs, mesolophids, and ectolophids were not observed in any specimens. A "pseudomesolophid" (Hershkovitz, 1962) was observed in several specimens of *interparietalis* on the lower first molar (two specimens [5.6%] from Isla San Lorenzo Norte and four [11.7%] from Isla San Lorenzo Sur). The mesoloph and mesostyle are rarely fused. This condition was observed on the M^1 in only two (7.1%) specimens of *stephani* and one (4.8%) of *eremicus* from Bahía de los

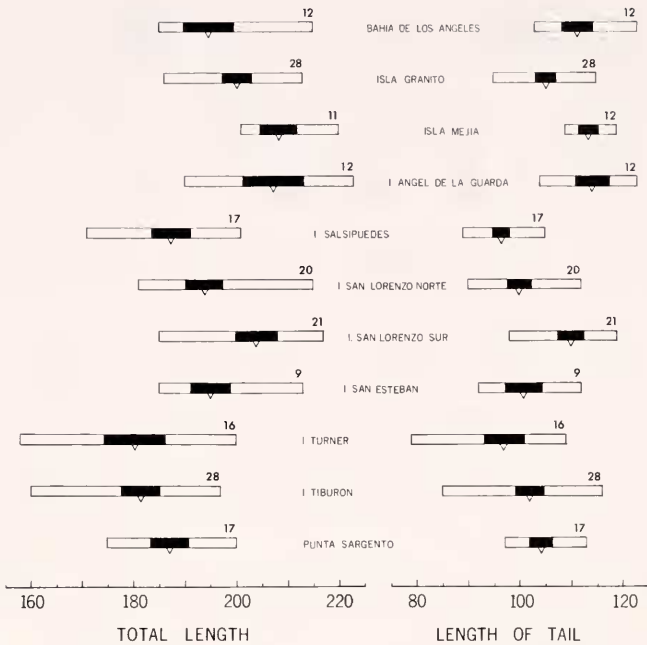


Figure 3. Geographic variation of two external dimensions of *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. The solid rectangles represent two standard errors on either side of the mean; hollow rectangles refer to the range of variation. Sample sizes are indicated for each plot.

Angeles.

Mice from the *guardia* and *interparietalis* groups of islands exhibit the simplest dental topography in the upper molars, owing to the absence or low frequency of mesostyles, particularly in the M^2 . Populations of *guardia* differ from *interparietalis* by the nearly complete absence of mesostyles and entostyles on the M^1 . In the lower molars there is little variation in frequency of ectostylids, but the mice from Isla Granito differ from the remainder of the island and mainland *Peromyscus* by virtue of the high frequency of mesostylids there.

On the basis of dental structures *Peromyscus* from Islas Granito and San Esteban are the most distinct of the island forms. In addition to possession of mesostylids, the mice from Isla Granito have a high frequency of mesolophos on M^1 . Also, a mesoloph on the M^2 was noted in 20.8% of the specimens; except for its occurrence at very low frequency in the population from Bahia de los Angeles, this structure was not observed on the M^2 in specimens from other localities. The mice from San Esteban resemble those from Granito in having a high frequency of mesolophos on the M^1 . However, the population differs from that on Isla Granito by the absence of mesolophos on the M^2 and the presence of mesostyles on the M^1 in 25.0% of the specimens. In general, populations from Islas Turner and Tiburon resemble mainland populations of *eremicus*.

Little phylogenetic information can be derived from the variation in dental patterns. For comparison, two mainland populations of *eremicus* from Bahía Kino and Punta Sargento, Sonora, show as much variation in frequencies of mesostyles, entostyles, and ectostylids as do all other island and mainland populations studied; yet, these mainland localities are only 30 miles apart. Note also the variation in dental structure among the

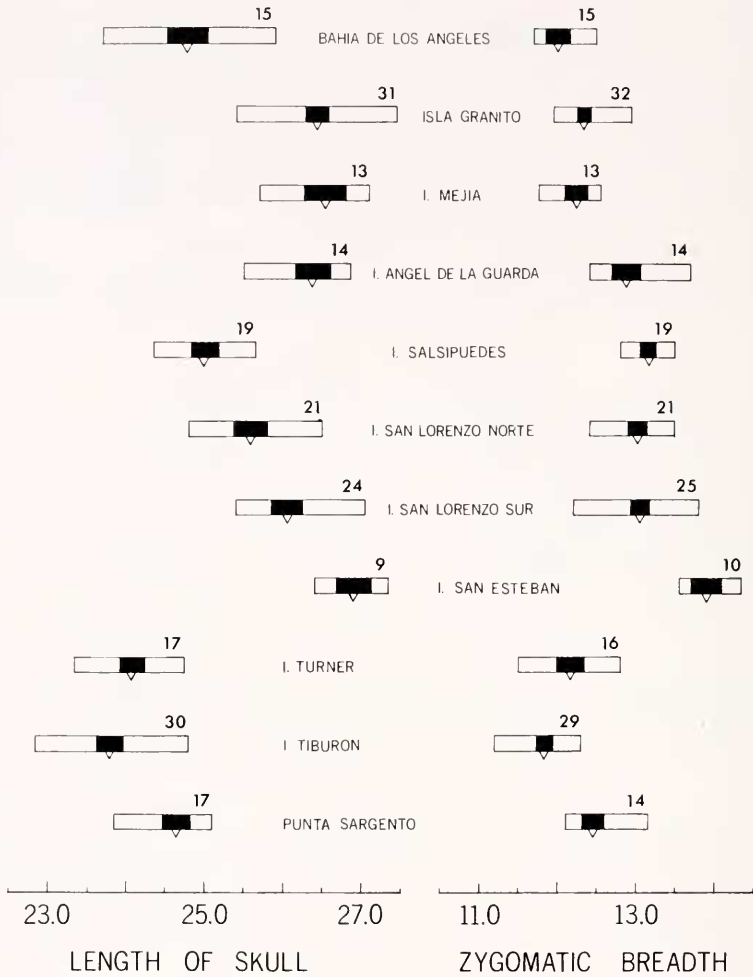


Figure 4. Geographic variation of two cranial dimensions of *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. For explanation of plots see Fig. 3.

three populations of *guardia* (Figs. 6 and 7, Table 1). Similar variation was noted in several species of *Peromyscus* by Hooper (1957). His results for *eremicus* correspond closely to those presented for populations of that species here.

QUALITATIVE CHARACTERS

Osteology. — Variation in osteological characters among *Peromyscus* commonly is subtle, and distinct character differences often are difficult to detect in closely related species. The skulls of six island and mainland examples studied here are illustrated in Fig. 8. Eight cranial features of taxonomic importance were discernible in the island and mainland forms. Many of these features were observed by Banks (1967). The characters and their character states are as follows:

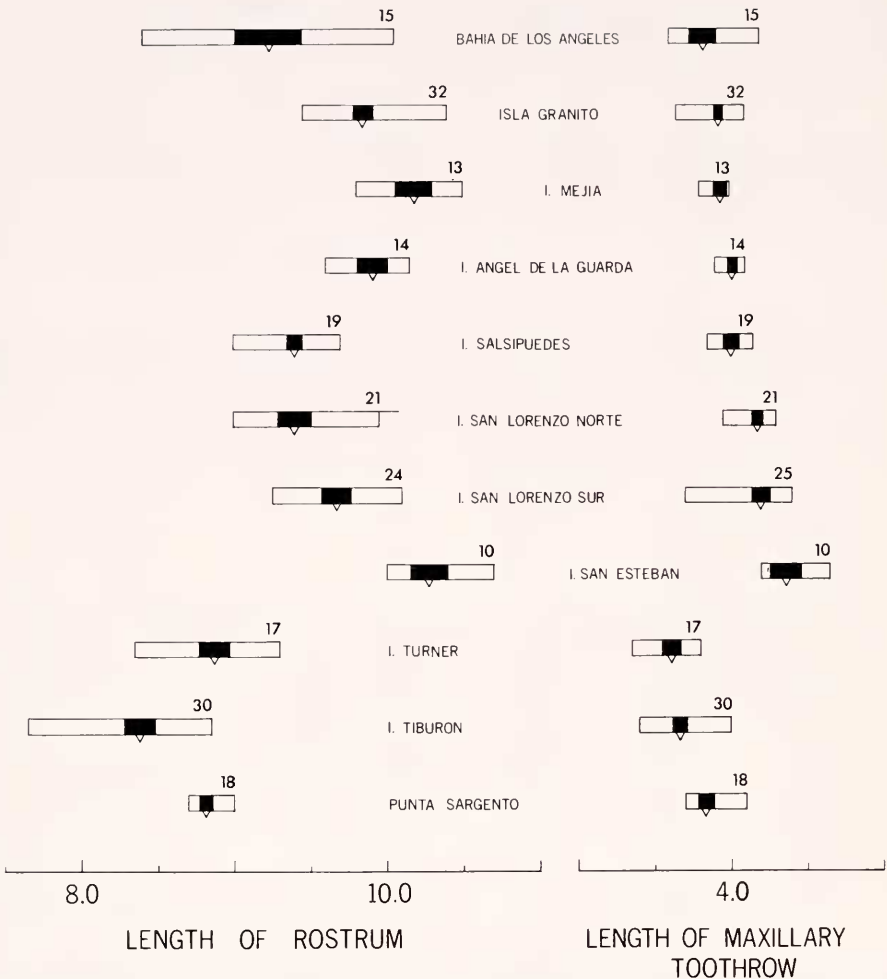


Figure 5. Geographic variation of two cranial dimensions of *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. For explanation of plots see Fig. 3.

(I) *Shape of frontal bone* (Fig. 8). — The posterior margin of this bone is curved (coded 0) in most of the island and mainland mice, but in certain populations (*stephani*, *boylei*) it usually is sharply angular (coded 1).

(II) *Position of nasal bones*. — In *stephani* and *boylei* the nasals extend posteriorly to or beyond the premaxillaries (0) (Fig. 9A'), while in all other populations the nasal bones do not reach the level of the posterior extension of the premaxillaries (1) (Fig. 9A).

(III) *Shape of posterior margin of nasals*. — The posterior margin of the two nasal bones is rounded or bluntly pointed (0) (Fig. 9A'), or squared (1) (Fig. 9A). This character is variable among mice on the eastern Gulf islands and among mainland populations of *eremicus*. Squared nasals are particularly prominent among the three populations of *interparietalis*.

(IV) *Shape of interparietal bone*. — Mice from populations of *guardia* exhibit a

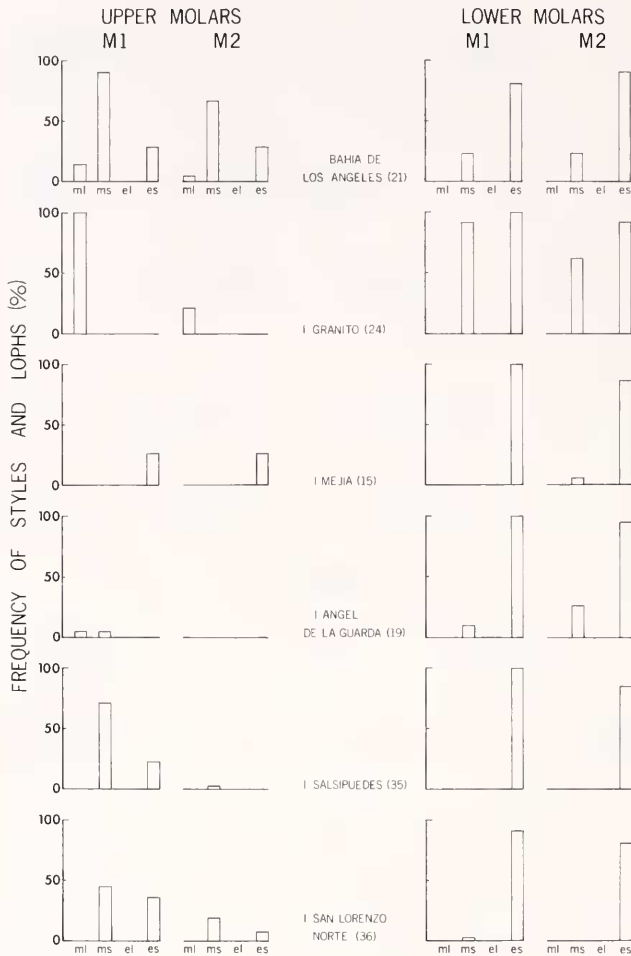


Figure 6. Frequencies of styles (styliids) and lophi (lophiids) among *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. Sample sizes are indicated in parentheses. Data for additional mainland populations are presented in Table 1.

relatively small, triangular interparietal bone (0) (Fig. 9B), while the bone in remaining insular forms generally is strap-shaped (1) (Fig. 9B' and B'').

(V) *Lateral bony extensions of interparietal* (Fig. 9). — Populations of *guardia*, *boylei*, and *stephani* commonly have small bony extensions of the interparietal bone that extend outward on each side toward the squamosals (1). The remaining island and mainland populations almost always lack these elements (0).

(VI) *Position of squamosals*. — *P. interparietalis*, *stephani*, and *boylei* from Isla San Pedro Nolasco have relatively flattened skulls. The squamosal bones in these forms are slanted dorso-medially (1). This trait is not evident (0) in other populations examined and the skulls are inflated. This trait is indicated in Fig. 8 by the enlarged appearance of the squamosals.

(VII) *Shape of mesopterygoid fossa*. — In most island and mainland forms the pterygoid bones adjacent to the fossa are straight (0) (Fig. 9C), but in *guardia* (Fig. 9C') the

lateral pterygoid margins of the fossa are usually concave and as a result the fossa appears larger and is expanded laterally (1). The mainland population of *eremicus* from Presa Obregon, Sonora, also exhibits the latter feature. The occurrence of an expanded mesopterygoid fossa varies geographically within species.

(VIII) *Position of incisive foramina.* — The incisive foramina in populations of *interparietalis*, *collatus*, and certain *eremicus* commonly extend posteriorly beyond the level of the first molars (1) (Fig. 9C), while in other populations the posterior termination of the foramina is usually anterior to the molar toothrow (0) (Fig. 9C'). The values for this character are quite variable geographically.

Table 1. Frequencies of occurrence of styles (stylids) and lophi (lophids) among some mainland populations of *Peromyscus eremicus* not included in Figs. 6 and 7. Entolophi (upper molars) and mesolophids and ectolophids (lower molars) were not observed in any specimens. Localities are arranged in order according to their number designation in Fig. 1. Numbers in parentheses identify sample sizes.

Locality		Upper Molars			Lower Molars	
		Mesoloph	Mesostyle	Entostyle	Mesostylid	Ectostylid
<i>Baja California</i>						
Turtle Bay (6)	M1	0.0	83.3	0.0	0.0	50.0
	M2	0.0	16.7	0.0	0.0	50.0
Barril (10)	M1	0.0	80.0	0.0	0.0	90.0
	M2	0.0	70.0	10.0	0.0	60.0
San Francisquito (14)	M1	7.1	100.0	21.4	0.0	85.7
	M2	0.0	64.3	7.1	0.0	85.7
El Marmol (10)	M1	0.0	70.0	0.0	0.0	100.0
	M2	0.0	30.0	0.0	0.0	100.0
San Telmo (7)	M1	14.3	85.7	0.0	14.3	71.4
	M2	0.0	85.7	0.0	0.0	71.4
<i>California</i>						
Escondido (13)	M1	0.0	92.3	7.7	0.0	84.6
	M2	0.0	69.2	0.0	0.0	46.2
<i>Sonora</i>						
Puerto Peñasco (19)	M1	0.0	89.5	36.8	0.0	94.7
	M2	0.0	73.7	26.3	0.0	89.5
Imuris (9)	M1	0.0	66.7	0.0	0.0	88.9
	M2	0.0	11.1	0.0	0.0	88.9
Puerto Libertad (18)	M1	0.0	56.7	50.0	0.0	61.1
	M2	0.0	38.9	38.9	0.0	100.0
Presa Obregon (11)	M1	0.0	63.6	9.1	0.0	100.0
	M2	0.0	9.1	0.0	0.0	91.0

Mean values for coded character states are presented in Table 2. Although mean values of certain characters exhibit considerable geographic variation (see above) they have been included here to demonstrate the osteological variation that exists among different populations of certain species relative to that between species. Criteria for weighting such features are discussed below.

It is evident that mice from Isla San Esteban are readily distinguishable from the remaining island populations on the basis of osteologic features. Further, *stephani* seems closest in these characters to *boylei*. Mice from the Guardia island group (*guardia*) are distinguishable chiefly by the triangular shape of the interparietal bone and the prominent

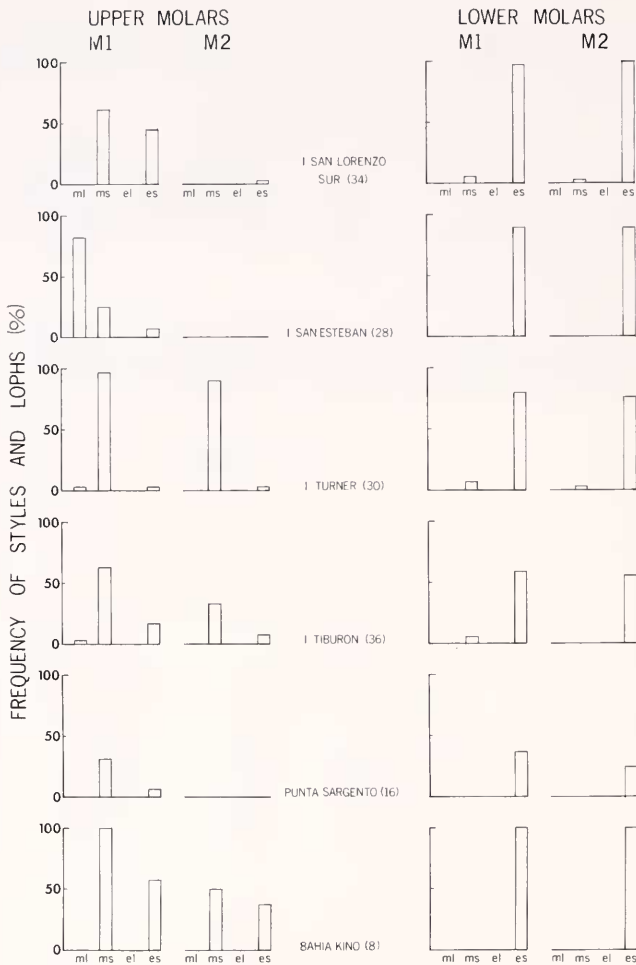


Figure 7. Frequencies of styles (stylids) and lophids (lophids) among *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. Sample sizes are indicated in parentheses. Data for additional mainland populations in Table 1.

lateral bony extensions of the interparietal, while those from the Lorenzo island group (*interparietalis*) differ from other island and mainland forms chiefly by the squarish posterior margin of the nasals and the flattened braincase. The forms from Islas Turner (*collatus*) and Tiburon (*eremicus tiburonensis*) closely resemble mainland *eremicus* in all features.

Post-cranial skeletons of all island and several mainland populations were examined, but no important variation in shape or position of bones was evident. However, differences in number of caudal vertebrae were observed (Fig. 10). Mice from mainland populations are more variable in this feature than those from the islands. In certain populations (e. g., *guardia*) the number of caudal vertebrae seems to be fixed. However, sample sizes generally are small, and conclusive statements must await additional data.

Pelage. — Three pelage features were discernible. These characters and their character

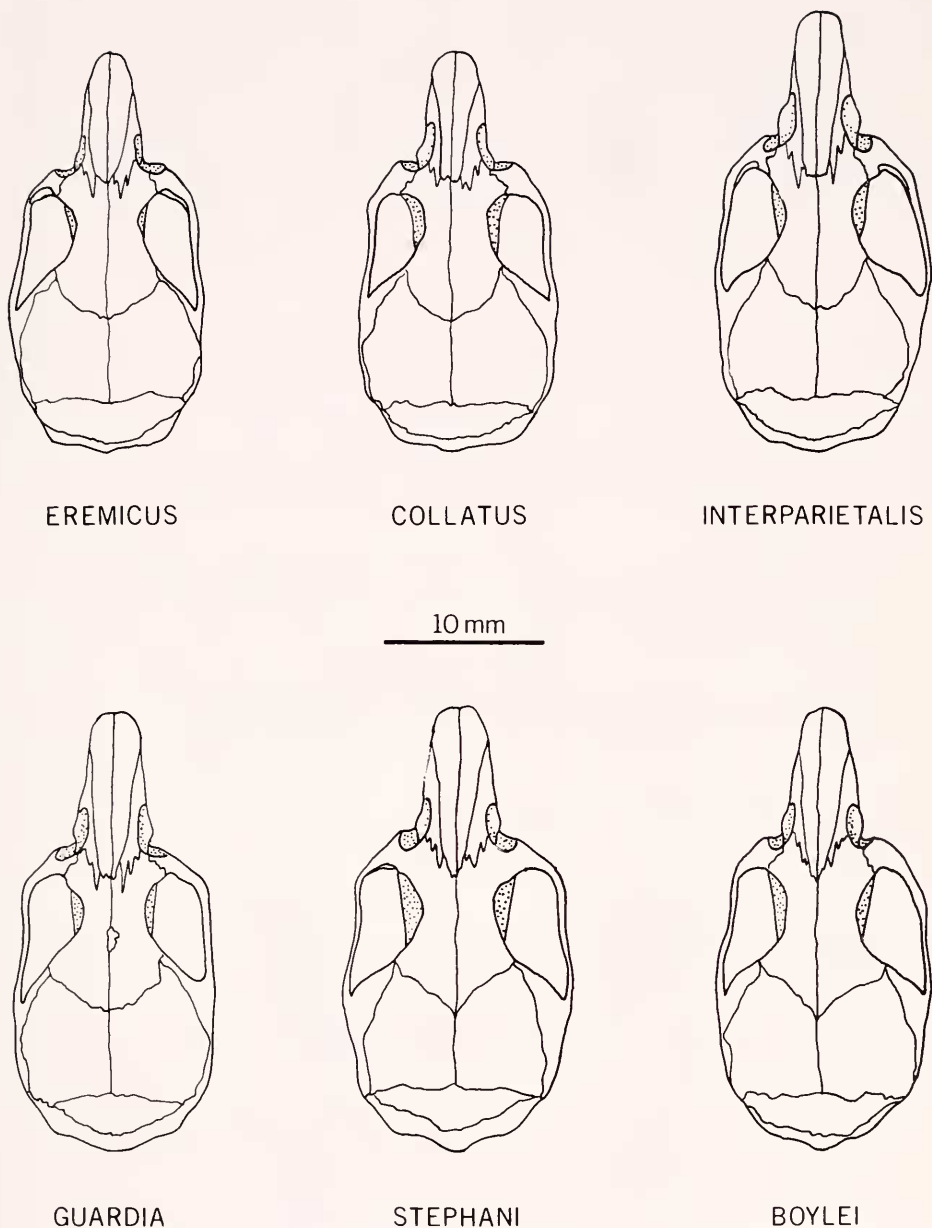


Figure 8. Dorsal skull views of six examples of *Peromyscus* from areas in and adjacent to the northern part of the Gulf of California, Mexico.

states are as follows: (IX) extent of tegumentary attachment on the tail (skin tightly attached to underlying tissue, 0; skin loosely attached and easily removed, 1); (X) hairiness of the tail (scantly haired, 0; well haired, 1); (XI) occurrence of gray facial coloration (absent, 0; present, 1).

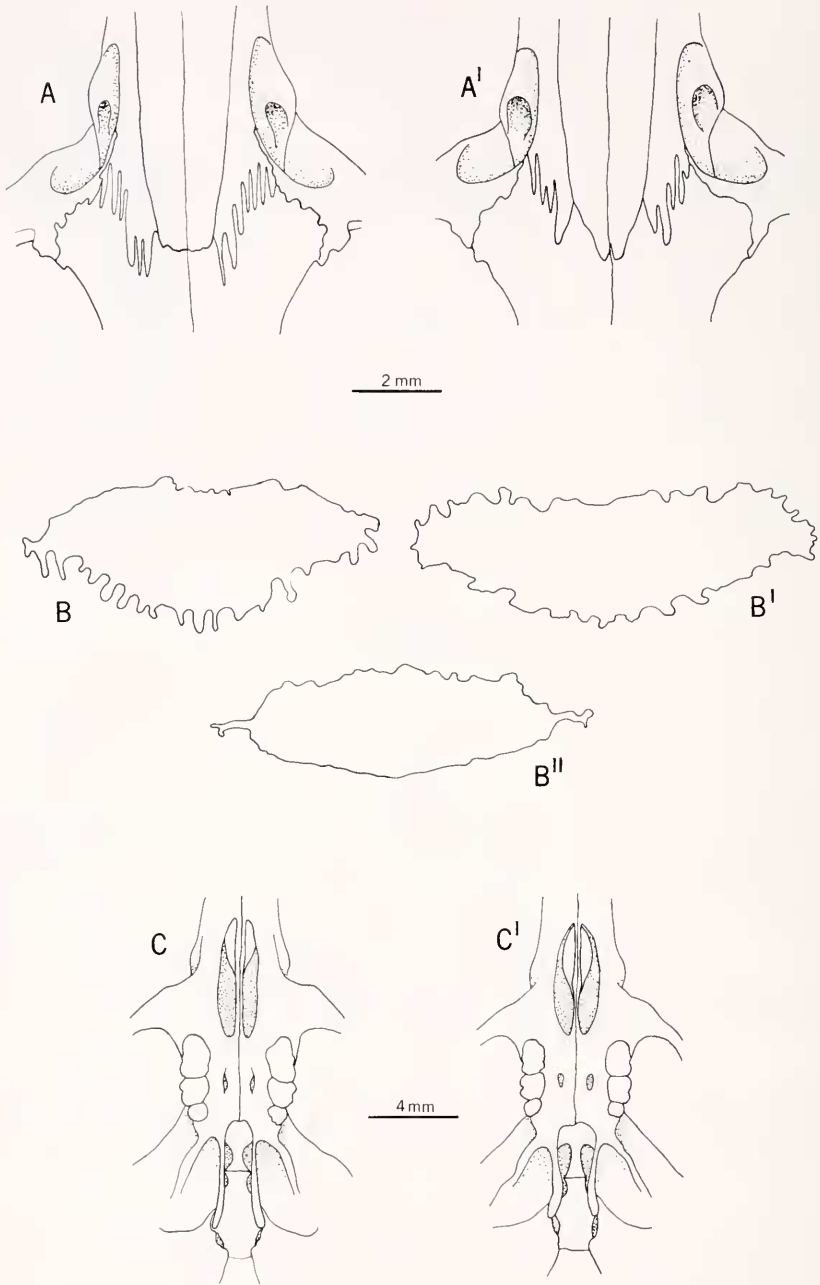


Figure 9. Views of: the dorsal aspect of the frontal region of the skull in *Peromyscus interparietalis* (A) and *P. stephani* (A'); interparietal bones of *P. guardia* (B), *P. interparietalis* (B'), and *P. stephani* (B''); and midventral region of the skull in *P. interparietalis* (C) and *P. guardia* (C'). For characters pertinent to these illustrations see text.

Table 2. Distribution of mean values of morphologic character states among island and mainland populations of *Peromyscus* in the northern part of the Gulf of California. Character states are discernible from Figs. 8-16 or are discussed in text. Roman numerals correspond to character designations given in text and in tables on file with NAPS (see text). Characters that are invariant within populations are not included here; for character state values of these characters see text. Sample sizes are listed for serologic and karyologic analyses.

Species and Locality	N	Osteology						Pelage			Phallus			N	Serology	♂, ♀ N Karyology			
		Shape of frontal (I)	Position of nasals (II)	Shape of posterior margin of nasals (III)	Shape of interparietal (IV)	Occurrence of lateral bony extensions of interparietal (V)	Position of squamosals (VI)	Shape of mesapterygoid fossa (VII)	Position of incisive foramina (VIII)	N	Occurrence of gray on face (XI)	N	Occurrence of ventral lappets (XIII)				Shape of baculum (XVI)		
<i>guardia</i> :																			
Granito	32	0.00	1.00	0.00	0.00	0.45	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00	9	0.00	0.00	15	2, 2
Mejia	13	0.00	1.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	4	0.00	0.00	3	1, 1
Angel de la Guarda	14	0.00	1.00	0.00	0.07	0.57	0.00	1.00	0.00	0.00	0.14	0.00	0.00	0.00	5	0.00	0.00	3	1, 1
<i>interparietalis</i> :																			
Salspuedes	19	0.00	1.00	1.00	1.00	0.05	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.86	7	0.86	1.00	17	2, 2
San Lorenzo Norte	21	0.00	1.00	1.00	1.00	0.00	1.00	0.00	1.00	0.00	0.76	0.00	0.00	0.00	6	0.00	1.00	21	3, 2
San Lorenzo Sur	25	0.00	1.00	0.88	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	8	0.00	1.00	15	2, 1
<i>collatus</i> : Turner	17	0.00	1.00	0.41	1.00	0.00	1.00	0.29	1.00	0.00	1.00	0.00	1.00	0.00	6	0.00	1.00	11	1, 1
<i>eremicus</i> :																			
Tiburon	28	0.00	1.00	0.25	1.00	0.00	1.00	0.00	0.00	0.00	0.93	0.00	0.93	0.00	4	0.00	0.50	5	2, 1
Bahia Kino	6	0.00	1.00	0.50	1.00	0.00	1.00	0.00	0.00	0.00	0.67	0.00	0.67	0.00	6	0.83	3.00	12	2, 1
Presa Obregon	10	0.00	1.00	0.20	1.00	0.00	1.00	0.00	0.00	0.00	0.20	0.00	0.20	0.00	10	0.90	4.00	4	1, 2
Bahia de los Angeles	15	0.27	1.00	0.27	0.87	0.00	0.00	0.00	0.00	0.00	0.53	0.00	0.53	0.17	19	0.61	1.00	18	2, 2
<i>merriami</i> :																			
Presa Obregon	17	0.00	1.00	0.76	1.00	0.06	1.00	0.12	0.00	0.00	0.00	0.12	0.00	0.00	16	1.00	0.00	5†	2, 2†
<i>stephani</i> :																			
San Esteban	10	1.00	0.00	0.00	1.00	1.00	1.00	0.10	1.00	1.00	0.40	0.10	0.40	1.00	3	1.00	0.00	9	2, 2
<i>boylei</i> :																			
San Pedro Nolasco	5	1.00	0.00	0.00	1.00	0.20	1.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	3	1.00	0.00	3	1, 1
near Tucson*	21	0.24	0.00	0.00	0.95	0.76	0.99	0.14	0.33	0.21	0.00	0.14	0.33	2.00	2	1.00	0.00	18	2, 2
<i>crinitus</i> :																			
California*	26	0.00	0.19	0.00	1.00	0.15	0.00	0.40	0.93	0.26	0.00	0.40	0.93	2.00	6	1.00	0.00	—	—

*For precise locality designation, see section on specimens examined.

†From near Tucson; see section on specimens examined.

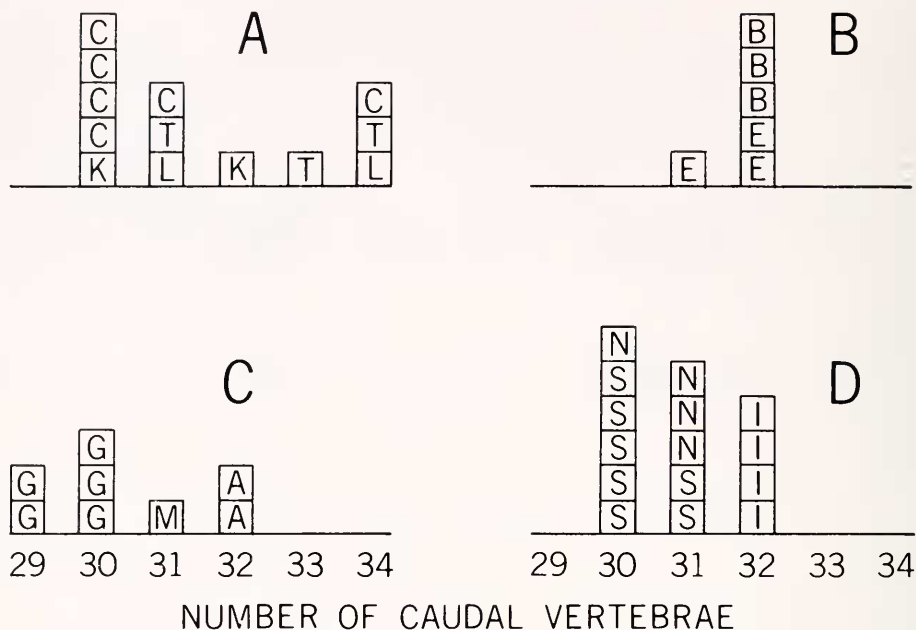


Figure 10. Number of caudal vertebrae in populations of *P. eremicus* and *P. collatus* (A), *P. boylei* and *P. stephani* (B), *P. guardia* (C), and *P. interparietalis* (D). Letter designations are as follows: A — Isla Angel de la Guarda; B — *P. boylei*; C — I. Turner; E — I. San Esteban; G — I. Granito; I — I. San Lorenzo Sur; K — Bahía Kino; L — Bahía de los Angeles; M — I. Mejía; N — I. San Lorenzo Norte; S — I. Salsipuedes; T — I. Tiburon.

Pelage characters serve chiefly to distinguish *stephani* and *boylei* from other forms. Only in *stephani* and *boylei* is the tail well haired and loosely attached. Pelage coloration is similar among the island and mainland mice, except that mice from Isla Mejía and Presa Obregon, where dark substrates occur, are darker than other populations. Few other pelage differences are found among the remaining populations, although certain populations (e.g., mainland *eremicus*) show considerable variation in the expression of gray on the face (Table 2).

Morphology of phallus. — The island populations exhibit both complex and simple peromyscine phallic types (Figs. 11 and 12). Phalli of specimens from Isla San Esteban (*stephani*) are complex and closely resemble *boylei* in all features. Those of the remaining island forms and mainland *eremicus* are relatively simple. Accouterments, such as ventral and dorsal lappets, protrusible tip of glans, and cartilaginous tip of baculum, are poorly developed or absent.

Specimens from the *guardia* group of islands have phalli that are morphologically intermediate between complex and simple types. A protrusible tip is present but not well developed, and dorsal lappets and a small cartilaginous tip also are present. Phalli of forms from Islas Tiburon and Turner, and the Lorenzo island group (*interparietalis*), closely resemble mainland *eremicus*, except that phalli of *interparietalis* are larger and six of seven *interparietalis* from Isla Salsipuedes and one of six *eremicus* from Bahía de los Angeles, Baja California, have ventral lappets (see Fig. 11 and Table 2). It is not clear whether these structures in the two latter populations are homologous, however, because the lappets in the specimen from Bahía de los Angeles are separated from the adjacent tissue by a simple

for *eremicus*, *crinitus*, and some populations of *maniculatus* by Brown and Welser (1968). The mobility for the three populations of *interparietalis* (ca. 94) also differs from the other forms studied here. In addition, the mobility obtained for albumin in *boylei* and *stephani* (90) does not correspond to the value (84) given for one individual of *boylei* by Brown and Welser, suggesting that an albumin polymorphism may exist in that species. Jensen (pers. comm.) has noted polymorphisms of albumin in *boylei* from northern Arizona. No intra-population variation was noted in this study.

Although direct comparisons are not possible, the positions of the albumin band in *interparietalis* and *guardia* correspond favorably to densitometer tracings of this band (Brand and Ryckman, 1969) except that those authors report a difference between albumin of *interparietalis* from Isla Salsipuedes and from the San Lorenzos (a mixed sample from San Lorenzo Sur and San Lorenzo Norte). Further investigation of this discrepancy is required.

Karyology.— All members of the genus *Peromyscus* so far examined have a diploid number of 48 chromosomes regardless of the proportion of acrocentrics in the complement (Hsu and Arrighi, 1966, 1968). The populations studied here are no exception. There also is considerable variation between species as regards morphology of the chromosomes. The populations examined here differ in the following characters (sample sizes given in Table 2):

(XXV) *Number of autosomal acrocentrics*.— There are no acrocentric chromosomes in *merriami*, *eremicus*, *interparietalis*, and *collatus* (0); most are either submetacentric or subtelocentric. *P. guardia* has one pair of small acrocentrics (1), while *stephani* and *boylei* each has 20 pairs (2).

(XXVI) *Morphology of the X chromosome*.— In most populations, including *merriami*, *eremicus*, *interparietalis*, *stephani*, *boylei*, and *guardia*, this chromosome has unequal arms (0). Most have a large submetacentric X chromosome, but in *guardia* from Isla Mejía it is a large subtelocentric. *P. collatus* has a large metacentric X chromosome (1). The morphology of this chromosome is subject to some variation both locally and geographically. For example, in *eremicus* it occasionally appears almost as a metacentric (cf. Hsu and Arrighi, 1968), whereas in *guardia* it varies from a submetacentric to subtelocentric condition. Although this character is employed beyond for purposes of assessing overall similarity, additional data may prove it to be unsuitable for taxonomic use.

(XXVII) *Morphology of the Y chromosome*.— This chromosome is a medium-sized acrocentric (0) in *guardia*, has unequal arms (1) in *eremicus* and *merriami* (medium subtelocentric), *interparietalis* and *collatus* (medium submetacentric), and is a medium metacentric in *stephani* and *boylei* (2). Hsu and Arrighi (*loc. cit.*) reported that the one individual of *eremicus* from Isla Tiburon they examined had a small acrocentric Y chromosome. However, examination of a photograph of that karyotype reveals that this chromosome is a subtelocentric according to the classification used here.

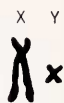
The fundamental numbers of chromosomes in the island and mainland forms are: *guardia* 90, *interparietalis* 92, *collatus* 92, *eremicus* 92, *merriami* 92, *stephani* 52, *boylei* 52. Karyotypes are illustrated in Figures 15 and 16.

BREEDING

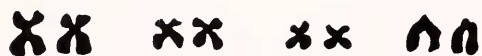
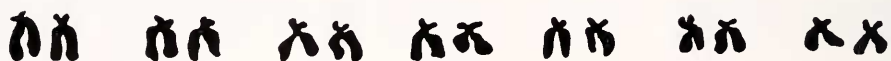
Attempted matings between different island and mainland forms are given in Table 3. The breeding colony of *interparietalis* from Islas Salsipuedes and San Lorenzo Norte was obtained in 1967. Consequently more matings of those populations were made. Unless otherwise noted, results of crosses in the following discussion refer also to reciprocal



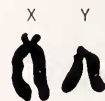
STEPHANI



BOYLEI (TUCSON)



GUARDIA (I. MEJIA)



GUARDIA (I. GRANITO)



Figure 15. Karyotypes of *P. stephani* and *P. guardia* from Isla Mejía; and sex chromosomes of *P. boylei*, and *P. guardia* from Isla Granito.

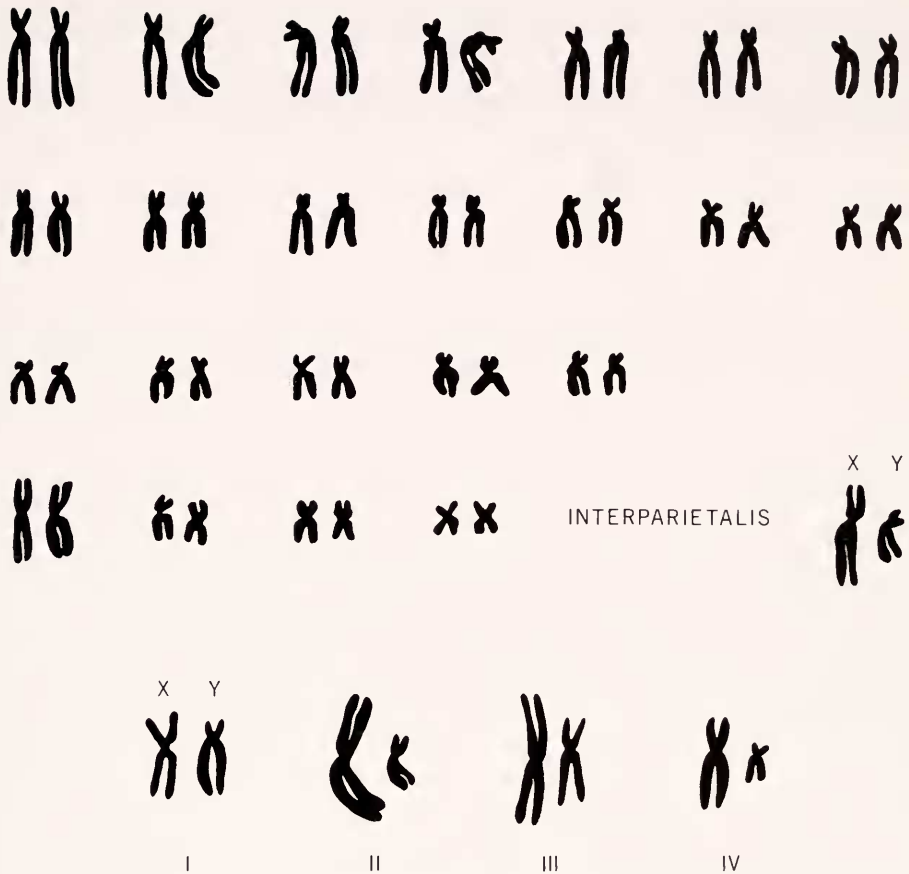


Figure 16. Karyotype of *P. interparietalis* and sex chromosomes of *P. eremicus* from Bahía de los Angeles (I) and Isla Tiburon (II), *P. collatus* (III), and *P. merriami* (IV).

matings. All island forms of *interparietalis* bred freely among themselves, and one cross of *interparietalis* (♀) and *collatus* (♂) was successful. In each case the offspring were viable. There was no success at breeding *stephani*, *boylei*, *guardia*, Tiburon *eremicus*, or *collatus* (except with *interparietalis*), even among controls. *P. eremicus* crosses, including one of Kino (♀) × Bahía de los Angeles (♂), produced viable offspring in all cases.

These results correspond well with data on attempted matings reported by Brand and Ryckman (1969); they were able to breed *interparietalis* and *eremicus*, but had very little success with *guardia*. The data indicate that certain island and mainland populations of *eremicus*, *interparietalis*, and *collatus*, are interfertile and are closely related. No conclusive statements can be made concerning the negative breeding evidence for populations of *guardia*, *eremicus tiburonensis*, *stephani*, and *boylei*. Morphological features, such as those of the phallus, may act as physical barriers to hybridization with certain forms, *P. e. tiburonensis*, however, is obviously closely related to mainland *eremicus* and *collatus*; yet no mated pairs produced offspring.

Evidence regarding laboratory breeding must be viewed with caution, since pre-mating isolating mechanisms may break down under laboratory conditions. Nevertheless, since

certain forms have the potential for interbreeding in the wild, close relationship of those populations is evident.

Table 3. Attempted matings of island and mainland *Peromyscus*. Numbers in parentheses represent reciprocal crosses.

MALES	<i>eremicus</i> : Bahía Kino	Bahía de los Angeles	Tiburón	<i>collatus</i> : Turner	<i>guardia</i> : Angel de la Guardia	Granito	Mejía	<i>interparietalis</i> : Salsipuedes	San Lorenzo Norte	San Lorenzo Sur	<i>stephani</i> : San Esteban	<i>boylei</i> : San Pedro Nolasco	near Tucson
FEMALES													
<i>eremicus</i> :													
Bahía Kino	1 2(1)	1(0)	2(1)	—	1(1)	—	—	—	—	—	—	—	—
Bahía de los Angeles	3	—	1(1)	—	0(2)	—	—	2(1)	0(1)	—	—	—	—
Tiburón	—	2	1(1)	—	—	—	—	—	—	—	—	—	—
<i>collatus</i> : Turner	—	—	1	—	—	—	—	—	1(1)	—	—	—	—
<i>guardia</i> :													
Angel de la guardia	—	—	—	—	1	1(0)	—	—	—	—	—	—	—
Granito	—	—	—	—	—	2	1(1)	—	—	1(1)	—	—	—
Mejía	—	—	—	—	—	1	—	—	—	—	—	—	—
<i>interparietalis</i> :													
Salsipuedes	—	—	—	—	—	—	—	3	3(1)	2(1)	—	—	—
San Lorenzo Norte	—	—	—	—	—	—	—	—	6	2(3)	—	—	—
San Lorenzo Sur	—	—	—	—	—	—	—	—	—	1	—	—	—
<i>stephani</i> :													
San Esteban	—	—	—	—	—	—	—	—	—	—	2	0(1)	1(1)
<i>boylei</i> :													
San Pedro Nolasco	—	—	—	—	—	—	—	—	—	—	—	1	—
near Tucson	—	—	—	—	—	—	—	—	—	—	—	—	2

EVOLUTION OF THE ISLAND FORMS
PHYLETIC RELATIONSHIPS

A total of 27 serologic, karyologic, osteologic, and other morphologic characters was treated by numerical taxonomic methods, first by a phenetic clustering technique, and then by the quantitative phyletic method (Kluge and Farris, 1969). The first step is the construction of a Prim Network (Prim, 1957; Kluge, in press; see also Edwards and Cavalli-Sforza, 1964) in which only phenetic differences (*sensu* Farris, 1967) between the island and mainland populations, or OTU's (Operational Taxonomic Units; see Sokal and Sneath, 1963), are determined. Two Prim Networks are presented (Figs. 17 and 18). The character states used to describe the OTU's are sample means (data for every character were not available for all individual specimens). Distances between OTU's (interval lengths) represent the sums of character differences between OTU's. The Prim Network connects the OTU's with minimum total interval lengths. There is no directionality implicit in the network, and angles of branching events are arbitrary. The first network (Fig. 17) includes data derived from all but serologic and karyologic characters. The second network (Fig. 18) includes only those populations for which complete data were obtained (sufficient data regarding characters of chromosomes and blood proteins were not available for *crinitus*).

Data regarding phalli for *crinitus* and mainland *boylei* and blood proteins and

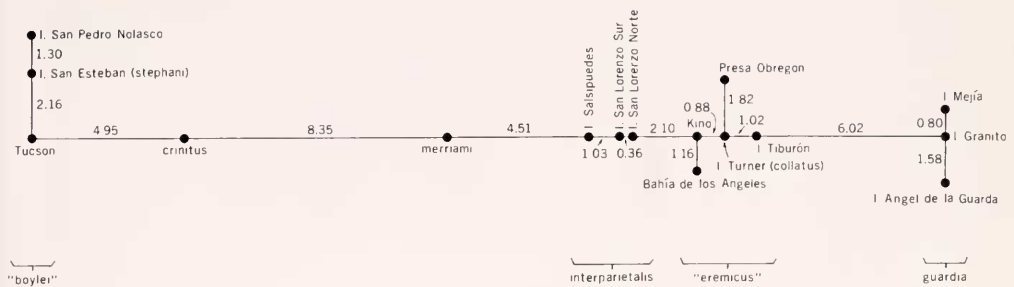


Figure 17. Prim Network computed from data derived from osteology, phallic morphology, pelage, and soft anatomy in *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. The interval lengths represent *unweighted* measures of the sums of character differences between OTU's. The network length is 38.04.

karyotypes for *merriami* were obtained from different populations than were data for other features in those species. Their inclusion is justified for comparative purposes because the above characters are relatively invariable geographically, and because even considerable variation in the above structures alters only the interval length and not the branching sequences. Consequently, the data are assumed to be representative.

Four distinct clusters are evident in each diagram: (1) a group consisting of populations of mainland *eremicus* and insular forms from Tiburón and Turner (labeled "*eremicus*"); (2) a cluster comprised of the three island populations of *interparietalis*; (3) a group composed of the three island forms of *guardia*; and (4) a group consisting of mainland and island *boylei* (Tucson and Isla San Pedro Nolasco) and the population from Isla San Esteban (*stephani*) (labeled "*boylei*"). The populations of *crinitus* (Fig. 17 only) and *merriami* are located intermediate to *boylei*- and *eremicus*-like forms on the networks.

The degree of phenetic similarity between the *boylei*-like forms and the remaining island and mainland forms clearly separates the former populations from the latter. They evidently are distantly related. Without doubt, *stephani* exhibits closest affinities to *boylei*. To my knowledge, *boylei glasselli* (Isla San Pedro Nolasco) and *stephani* comprise the only two island derivatives of *boylei* in the Gulf. Note the differences in the Prim Networks, especially for populations of *interparietalis* and *eremicus*, that result from the addition of data on serology and karyology.

In the quantitative phyletic method a Wagner Diagram (Farris, 1970) was used to depict interval lengths (patristic differences; *sensu* Farris, 1967) and branching events (Fig. 19). The Wagner Diagram differs from the Prim Network in three ways: (1) each character is weighted *a priori* by the mean value of the reciprocal of the intrapopulation standard deviation over all OTU's (i.e., conservative characters are more heavily weighted; see Farris, 1966; Kluge and Farris, 1969); (2) hypothetical intermediates are generated to minimize total interval length (i.e., to maximize parsimony); and (3) a hypothetical ancestor is chosen, thus giving directionality to the diagram¹. The intervals on the diagram represent the sums of *weighted* character differences between OTU's.

Populations representing *eremicus*, *merriami*, *interparietalis*, *collatus*, and *guardia* were examined for purposes of ascertaining phylogenetic relationships. These forms exhibit close morphologic and zoogeographic similarities and probably form a mon-

¹The character standard deviations, weighted character state values, and character state values for the hypothetical ancestor and generated intermediates, are filed with the National Auxiliary Publication Service of the American Society for Information Science, and may be obtained by ordering NAPS Document 01267 from ASIS National Auxiliary Publication Service, CCM Information Corp., 909 Third Ave., New York, N.Y. 10022, remitting \$5 per photocopy or \$2 per microfiche copy.

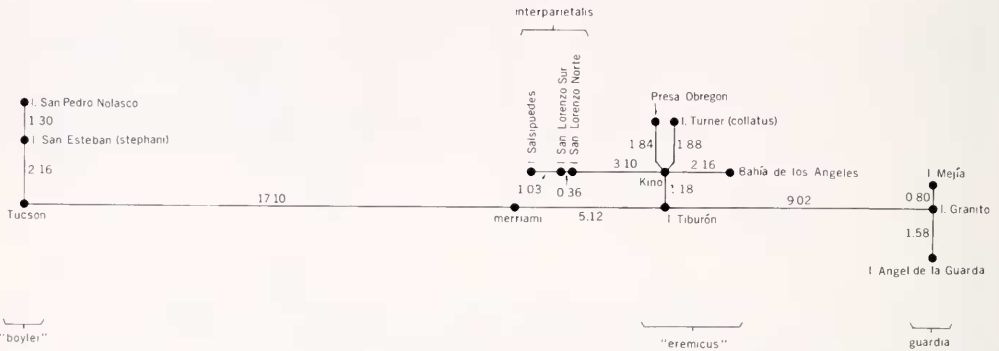


Figure 18. Prim Network computed from data derived from all coded characters (features in Fig. 17 plus data from serology and karyology) in *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. The interval lengths represent *unweighted* measures of the sums of character differences between OTU's. The network length is 48.63.

ophyletic group. They are evidently only distantly related to *boylei*, *crinitus*, and other continental species not studied in detail here. Nineteen of the original 27 characters were used in this analysis. The other eight characters (II, IX, X, XVIII, XIX, XX, XXII, and XXIV) serve only to distinguish *eremicus*-like forms from *boylei*-like forms. Characters of *Peromyscus eremicus* were chosen as ancestral for *eremicus*-like forms for the following reasons: (1) zoogeographically, *eremicus* represents the only species of *Peromyscus* that is present on the mainland of both sides of the Gulf, and it seems reasonable to assume that the island populations (excepting *stephani*) resulted from isolation of a mainland *eremicus*-like progenitor; and (2) the species shares the most characters in common with all the insular forms with the result that populations of this species are located centrally to other similar forms on the Prim Network. Assuming that evolution from a primitive ancestor takes place in more than one direction (i.e., it is radiative) and at approximately similar rates in major phyletic lines, then a population (or populations) located near the center of the Prim Network would seem to be the best approximation to the ancestral condition in the absence of unequivocal evidence. Thus, *eremicus*, or more likely a progenitor of similar characteristics, is here considered the ancestral type. Mean values of the character states for mainland populations of *eremicus* were given to the hypothetical ancestor.

From the available data, it is not possible to ascertain which mainland *eremicus* are most like the ancestral form; all populations, and particularly those of *P. e. eremicus*, which occurs on the coastal areas surrounding the northern portion of the Gulf, are very similar morphologically. The close phenetic similarities of mainland populations result in the compact cluster on the Prim Networks (Figs. 17 and 18). On zoogeographic grounds, however, it seems likely that western island populations are derived from Baja Californian *eremicus*, whereas populations on the eastern Gulf islands are probably derived from Sonoran *eremicus*. The affinities of other mammals on eastern and western Gulf islands correspond closely to mainland species of the eastern and western sides of the Gulf, respectively (Table 4). Similar relationships are shown by peromyscines on other Gulf islands (Lawlor, in press), and by the amphibians and reptiles in the Gulf (Soulé and Sloan, 1966).

It is clear from the phylogeny presented in Fig. 19 that, with the exception of *merriami*, *interparietalis* and *guardia* are the most divergent of the *eremicus*-like forms. Populations from Tiburón (*eremicus tiburonensis*) and Turner (*collatus*) are not far

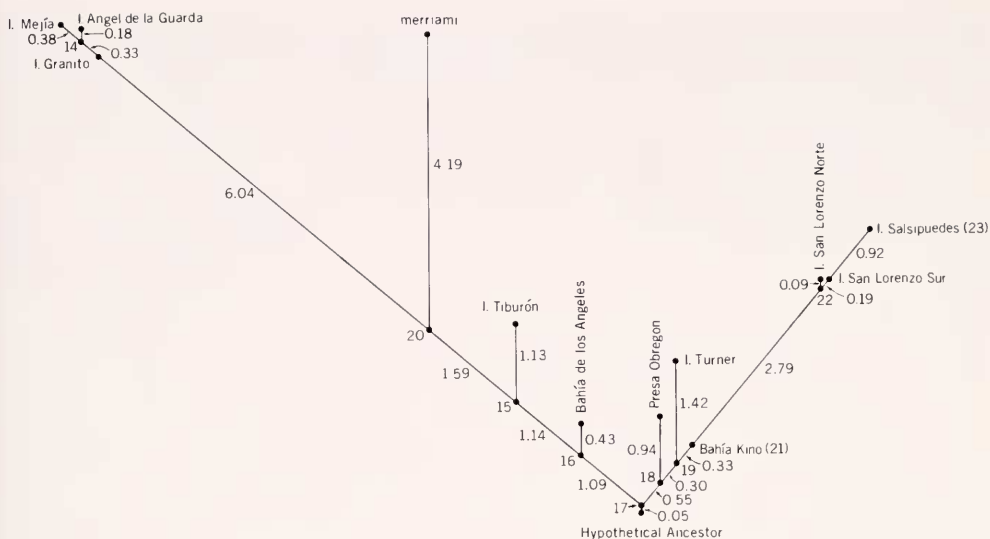


Figure 19. Wagner Diagram depicting the phylogeny of closely related *Peromyscus* on northern island and mainland areas in and adjacent to the Gulf of California, Mexico. The interval lengths represent *weighted* measures of the sums of character differences between OTU's. Character state values for hypothetical intermediates generated during computation of the phylogeny are on file with NAPS (see text). The total length of the dendrogram is 24.08.

removed from the hypothetical *eremicus* ancestor. *P. guardia* differs from other *eremicus*-like forms in characters that are relatively invariable within species. Examples are the presence of band C hemoglobin, a triangular interparietal bone, and characters of the phallus. Conversely, *interparietalis* differs chiefly in features that often exhibit a high variance within species, such as the position of squamosals and shape of the posterior margin of the nasals. For instance, an inflated braincase owing to the position of the squamosals is observed in one of the two *boylei* populations examined (Table 2). Because of these differences in character state variation, *guardia* is more divergent from *eremicus* than is *interparietalis*.

The phylogeny presented here as a working model can be used to examine evolutionary changes in certain characters. For example, according to Hooper and Musser (1964a) and Hershkovitz (1962) simple conditions of the phallus (in *Peromyscus* these include the absence of a protrusible tip, lappets, and a cartilaginous tip on the baculum) and of the dentition (e.g., absence of accessory styles and lophes on the molars) are generally thought to result from loss of structures present in a more complex progenitor. Patterns of overall historical changes in these structures among island *Peromyscus* may not parallel trends in rodents in general. Nevertheless, the trends do differ from current views on the subject: (1) In *guardia* there evidently has been selection favoring both decreased and increased complexity of the teeth. There has been a virtual loss of mesostyles in all populations while in two populations mesostyles are present, and on one island (Granito) the frequency is 100%. Selection has evidently acted to change the two structures independently and in opposite directions. (2) *P. guardia* also exhibits a relatively complex phallus (see above). A protrusible tip and dorsal lappets, although poorly developed when compared with those structures in *boylei* or *crinitus*, are present, which suggests that complex phalli can evolve from simple phalli. Also, mice from Isla Salsipuedes (*interparietalis*) have developed

ventral lappets. The evidence further indicates that acrocentric chromosomes are derived from bi-armed chromosomes in Gulf *Peromyscus*. In *guardia*, the Y chromosome and one pair of autosomes are acrocentric. No other island or mainland forms studied, other than *crinitus* (Hsu and Arrighi, 1968), *boylei*, or *stephani*, have acrocentric chromosomes, and in the latter species nearly the entire complement of chromosomes are acrocentric (only the sex chromosomes and three pairs of autosomes are bi-armed).

Whether the trends noted above are characteristic of evolutionary changes of these features in other peromyscines or in other rodents is a moot question, but this may be the case in the development of accouterments in the phallus of *P. eva* (Lawlor, in press). The trends may represent reversals from the normal pattern of change in *Peromyscus*. In any event, the overwhelming evidence based on overall similarity indicates that the phalli, dentition, and chromosomes of *guardia* and *interparietalis* did evolve in the above ways. If the alternative hypothesis is invoked, namely that *guardia* and *interparietalis* are considered derivatives of an ancestor having a complex phallus and dentition and a chiefly acrocentric chromosome complement (e.g., a *crinitus*-like form), then convergences of many other characters must have occurred (e.g., osteologic and pelage characters, etc.). The latter seems highly unlikely. Moreover, the probability is quite low that such convergences occurred in all three populations of *guardia* while in *stephani*, which occurs in seemingly similar habitat on an island that is as well isolated and is of approximately the same age, none are observed. I regard the similarities of *guardia* and *eremicus* as indicators of genetic relationship and view the derivation of *guardia* in the most parsimonious manner, namely that it is derived from an *eremicus*-like progenitor.

Evidence from morphology of chromosomes and male accessory reproductive structures suggests that *eremicus* and closely related species may share characters that are primitive for *Peromyscus*. Members of the subgenus *Haplomyomys* (excepting *crinitus*) are the only species having a complete complement of male accessory reproductive features (Linzey and Layne 1969). In all other species of the genus one or more elements are absent or vestigial. Except in *guardia*, acrocentric chromosomes are absent in mice of the subgenus. Although practically nothing is known about chromosome evolution in *Peromyscus*, particularly in view of the fact that Robertsonian fusion cannot be invoked (Hsu and Arrighi, 1966; 1968), the data at least are not inconsistent with the view that the presence of acrocentrics is a derived condition. Hsu and Arrighi (1968) presented a hypothetical phylogeny of *Peromyscus* that describes the evolution of chromosomes as resulting from a primitive acrocentric condition, but they noted (p. 437) that the phylogeny was presented in that manner principally for convenience, stating that chromosome evolution in *Peromyscus* may have occurred in either direction. Information on musculature (Rinker, 1963) also supports the view that *Haplomyomys* may be a primitive peromyscine group. Most of the conditions of the musculature that Rinker considered primitive are present in that subgenus. The evidence presented in this study suggests that complexities of the teeth and phallus derive from simple conditions and that acrocentric chromosomes derive from a bi-armed condition, at least in the species examined. Most of the *Haplomyomys* studied herein exhibit simple conditions of those structures. These data and those presented above support the contention of Linzey and Layne (1969) that *Haplomyomys* contains primitive members of the genus.

HISTORICAL PERSPECTIVE

The deserts of western North America, with which the origin and divergence of *P. eremicus* and related forms are closely associated, resulted chiefly from rain shadows produced by extensive mountain building in that area beginning in the Triassic and

continuing to the Pleistocene (King, 1958). However, adequate conditions to support lowland desert forms like *eremicus* probably did not exist prior to the formation of the North American deserts in mid-Pliocene (Axelrod, 1948). Undoubtedly these deserts were further modified by glacial advances and retreats during the Pleistocene, so that relatively stable desert conditions probably did not arise until early or middle Pleistocene, when successive glacial maxima became milder and interglacial periods were characterized by increasingly drier conditions. Displacement of desert elements by the Madro-Tertiary flora (e.g., thorn-scrub) during glacial advances in the early Pleistocene probably resulted in the separation of prototypes of *merriami* and *eremicus* and accounts for the differences in their habitat preferences today (Lawlor, in press).

The history of the Gulf of California is not well documented. Although certain authors (e.g., Durham and Allison, 1960) consider the Gulf to be as old as the Cretaceous orogeny in North America and that it reached its present configuration by the beginning of the Pliocene, recent investigations of the southern Gulf floor (Larson *et al.*, 1968; Moore and Buffington, 1968) suggest that the majority of crustal movement occurred since middle or late Pliocene. A proto-gulf is indicated, however, by earlier Pliocene fossil beds located in northern parts of the Gulf. In any case, the northern deep-water islands in the Gulf may not have originated until late Pliocene or early Pleistocene. For example, sedimentary beds of relatively recent deposition are known from the Lorenzos (early Pliocene) and Angel de la Guarda (late Pliocene) (Anderson, 1950), indicating that the islands were submerged in a shallow water embayment or saline lake at the time. The geologic relationships of these islands to adjacent submarine troughs suggests that the islands may have resulted partly from elevation along faults (Shepard, 1950). Part of this uplift was probably Pleistocene (*Ibid.*). The present separation of Islas Tiburon and Turner from the Sonoran mainland was likely attained with the last glacial retreat (*ca.* 15,000 years ago).

P. eremicus and related desert forms probably did not originate until formation of the deserts in mid-Pliocene. Consequently, evolution and radiation of this group on mainland and island areas has been relatively recent and no doubt has been substantially affected by displacement and expansion of the lowland deserts during the Pleistocene. In this connection, the suggested origin and radiation of these mice corresponds closely to that described for the lizard genus *Uta* (Ballinger and Tinkle, in press).

ZOOGEOGRAPHIC RELATIONSHIPS

Relationships between *guardia*, *interparietalis*, and *eremicus* are consistent with Banks' (1967) contention that *guardia* and *interparietalis* probably had separate origins from a mainland *eremicus*-like stock. Furthermore, *Peromyscus* has not been taken on two islands (Isla Partida and Raza) that are located between the two groups of islands supporting *guardia* and *interparietalis*, although several people have collected on each (I have collected only on Isla Partida). This suggests that *guardia* and *interparietalis* do not represent isolates of a form once continuously distributed among these islands, but rather that they are of separate mainland origin (*Ibid.*).

The time interval between initial isolation of the island populations from the mainland is probably the principal factor affecting the degree of divergence of northern island forms in the Gulf of California. This seems to be the case for the following reasons: (1) Morphological divergence is at least broadly related to temporal differences in island formation. Angel de la Guarda and its satellite islands, the Lorenzo group of islands, and San Esteban have been separated from the mainland for a considerable length of time. Islas Tiburon and Turner most certainly are no older than late Pleistocene. *P. eremicus*-like forms on the older groups of islands (*guardia* and *interparietalis*) are more divergent

than populations on younger islands (*eremicus tiburonensis* and *collatus*). (2) Apparently gene flow is minimal or absent among islands and between islands and the mainland. Differences persist among populations separated by very short distances, and because of habitat similarities and high population densities these differences probably are not attributable to presently existing differential selection coefficients or genetic drift. For example, it was pointed out above that populations from Islas San Lorenzo Sur and San Lorenzo Norte differ significantly ($P < .05$) in many morphometric characters; yet these islands are separated by 100 yards at most, and at low tide half-submerged rocks project above the water for almost the entire distance. Furthermore, ventral lappets on the phallus persist in most individuals of *interparietalis* from Isla Salsipuedes, while this feature evidently is absent in other nearby populations of that species. Isla Tiburon is separated from the Sonoran mainland by as little as two miles and by shallow water (only six meters at certain places); yet differences in phalli (and perhaps in karyotypes) are evident between the mice there and on the adjacent mainland (e.g., Bahía Kino); similar differences also persist between mice on Tiburon and those on Turner. In *guardia*, dramatic differences in dental patterns and morphometric characters are evident. It appears that distance effects owing to differential gene flow, although perhaps important in early colonization and establishment of the island populations, have been relatively unimportant in shaping present characteristics of the island forms. (3) Differences among island populations seemingly are not explicable only in terms of habitat differences. The northern part of the Gulf is marked by overall floral uniformity (Shreve and Wiggins, 1951; Felger, 1966). In addition, xeric rocky habitats are characteristic of all the islands inhabited by *Peromyscus*.

Table 4. Zoogeographic relations of species of mammals on northern islands in the Gulf of California. Only island species having mainland relatives on one side of the Gulf are compared. No mammals other than *Peromyscus stephani* and *Rattus norvegicus* are known from Isla San Esteban.

Locality	<i>Perognathus spinatus</i>	<i>Perognathus intermedius</i>	<i>Perognathus penicillatus</i>	<i>Neotoma lepida</i>	<i>Neotoma albigula</i>	<i>Dipodomys merriami</i>	<i>Lepus alleni</i>
Western islands:							
Granito	?			?			
Mejía	X			?			
Angel de la Guarda	X			X			
Salsipuedes	?						
San Lorenzo Norte	X						
San Lorenzo Sur	X						
Eastern islands:							
Tiburon		X	X		X	X	X
Turner		X ¹	?		X ²		
Mainland:							
Baja California	X			X			
Sonora		X	X		X	X	X

¹This population originally was described as *P. penicillatus* (Burt, 1932) but evidently is *intermedius* (Patton, pers. comm.)

²Called *N. varia*, but closely related to *albigula* (Burt, 1932)

On the basis of its degree of divergence and its phylogenetic relationships to *merriami*, *guardia* evidently has long been separated from an *eremicus*-like ancestor. A prototype of *merriami* is thought to have arisen in early Pleistocene (see above) and the cladistic relationship between *guardia* and *merriami* indicates that they probably share a common ancestry. Thus, *guardia* probably represents a derived form of a stock that gave rise to *merriami* and that also colonized Angel de la Guarda and satellite islands in the early Pleistocene. *P. interparietalis* evidently is more recently derived from a mainland *eremicus*-like form, possibly in middle to late Pleistocene. Mice from Islas Turner and Tiburon undoubtedly arose as a result of isolation of the two islands when the last major increase in sea level took place. *P. stephani* presumably has been isolated for some time (probably as long as *interparietalis*). It probably reached San Esteban from the eastern mainland during a glacial maximum in the Pleistocene when Isla Tiburon was part of the continent. Considering the present distribution of *boylei*, the initial colonization of Isla San Esteban by a *boylei*-like form was probably also associated with more mesic habitats at that time.

Early colonization and evolution of the island forms was likely erratic and unstable, and effects of distance between islands and the mainland, island area, and population size on genetic change were doubtless substantial. Once established, however, it appears that the island populations maintained their morphologic (and presumably genetic) integrity, and that the low rates of gene flow that obtain between the different island and mainland populations are unable to effect major changes in morphologic features.

The presence of a particular species on an island appears to me to result from historical accident. I cannot explain the absence of an *eremicus*-like form from an island like San Esteban, with its xeric, rocky habitat and floral composition similar to other Sonoran Gulf islands (Felger, 1966). Perhaps *eremicus* and *boylei*, or forms closely related to them, are competitors. Circumstantial evidence concerning the status of mice on Isla San Pedro Nolasco, where both *boylei glasselli* and an *eremicus*-like form (*pembertoni*) are known, suggests that *boylei* may be competitively superior to *pembertoni*. I collected there twice in the summer of 1967 and was unable to obtain *pembertoni*, although Burt (1932) took *pembertoni* and *boylei* in about equal numbers. This fragmentary information suggests that *boylei* may be supplanting *pembertoni* there, although the habitat, consisting of open slopes with cacti and low brush, and ravines of dense grass, is one of the most diverse of the northern islands.

If the above evidence is indicative of a competitive superiority of *boylei*-like forms, then *P. stephani*, owing to its occurrence on Isla San Esteban, may have acted as a barrier to dispersal of *eremicus*-like forms across the Gulf. Distinct morphologic differences do exist between eastern and western island *eremicus*-like forms (see above), suggesting few such crossings have been made.

TAXONOMIC CONCLUSIONS

I concur with Banks (1967) in considering *interparietalis* and *guardia* distinct from one another and from *eremicus*. Although *interparietalis* is evidently much less removed from the presumed *eremicus*-like ancestor than *guardia*, on morphologic and zoogeographic grounds it seems worthy of specific status. On the other hand, *collatus* (Isla Turner) is very similar to mainland and Tiburon *eremicus*. Excepting the difference in the X chromosome, differences that separate the two species are subtle and are reminiscent of geographic variation exhibited by mainland populations of *eremicus* (Lawlor, in press). The mice from Isla Turner should bear the name *P. e. collatus*. The relationships of *merriami* and *eremicus*, based on osteology and morphology of the phallus, are discussed

elsewhere (Lawlor, in press; see also Hoffmeister and Lee [1963], and Commissaris [1960]). The additional information regarding blood proteins and karyology and the phenetic and phylogenetic relations of the two species presented here support earlier conclusions that *merriami*, although morphologically distinct, exhibits close affinities to *eremicus* and is probably derived from a progenitor similar to that species. All of the above species are members of the subgenus *Haplomylomys*.

P. stephani clearly is a close relative of *boylei* and should be placed with *boylei* in the subgenus *Peromyscus*. In my view *stephani* should be retained as a species.

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SPECIMENS EXAMINED

Specimens employed for analysis of blood proteins and karyology were collected alive and maintained at the University of Michigan. Most of these mice are preserved in the Museum of Zoology, even though not cited below. Sample sizes and localities from which these specimens were obtained are given in the appropriate tables above. Only specimens obtained for purposes of examining morphologic features of the pelage, phalli, osteology, and soft anatomy are listed below. Where appropriate, numbers in parentheses identify the localities on the map (Fig. 1).

P. boylei.— ARIZONA: Marble Park, Catalina Mts., Pima Co. (9), 24 (UMMZ). SONORA: Isla San Pedro Nolasco (14), 7 (UMMZ).

P. crinitus.— CALIFORNIA: Paiute Creek, Inyo Mts., Inyo Co. 28 (UMMZ).

P. eremicus.— BAJA CALIFORNIA: Turtle Bay (1), 10 (3 SD, 3 USNM, 4 UMMZ); Barril (2), 10 (SD); Bahía de los Angeles (3), 23 (2 SD, 1 UCLA, 20 UMMZ); San Francisco (4), 16 (USNM); El Marmol (5), 14 (CAS); San Telmo (6), 7 (UMMZ). CALIFORNIA: Escondido, San Diego Co. (7), 21 (KU). SONORA: Puerto Peñasco (8), 20 (17 SD, 3 UA); Imuris (10), 9 (KU); Puerto Libertad (11), 20 (2 KU, 18 SD); Punta Sargento (12), 24 (UCLA); Bahía Kino (13), 14 (2 UA, 6 KU, 6 UMMZ); Presa Obregon (15), 13 (10 KU, 3 UMMZ); Isla Tiburon, 45 (4 CAS, 3 KU, 1 SD, 19 UC, 6 UCLA, 12 UMMZ); Isla Turner, 37 (1 CAS, 4 KU, 3 SD, 15 UCLA, 14 UMMZ).

P. guardia.— BAJA CALIFORNIA: Isla Angel de la Guarda, 28 (11 SD, 10 UCLA, 7 UMMZ); Isla Granito, 40 (7 SD, 33 UMMZ); Isla Mejia, 17 (5 CAS, 3 SD, 1 UCLA, 8 UMMZ).

P. interparietalis.— BAJA CALIFORNIA: Isla Salsipuedes, 48 (1 CAS, 13 SD, 34 UMMZ); Isla San Lorenzo Norte, 41 (19 SD, 22 UMMZ); Isla San Lorenzo Sur, 46 (7 UA, 11 CAS, 16 SD, 7 UCLA, 5 UMMZ).

P. merriami.— SONORA: Presa Obregon (15), 20 (17 KU, 3 UMMZ).

P. stephani.— SONORA: Isla San Esteban, 37 (2 CAS, 1 SD, 19 UCLA, 15 UMMZ).

The locality specified as "near Tucson" for *boylei* (Table 2) refers to Marble Park, Catalina Mts., Pima Co., Arizona, and Molino Canyon, 18 mi. NE Tucson, Catalina Mts., Pima Co., Arizona. The same designation (Table 2) for *merriami* refers to 3/4 mi. SE San Xavier Mission, Pima Co., Arizona.

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LAMPETRA (ENTOSPHEMUS) LETHOPHAGA,
NEW SPECIES, THE NONPARASITIC DERIVATIVE
OF THE PACIFIC LAMPREY

CARL L. HUBBS

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LAMPETRA (ENTOSPHEMUS) LETHOPHAGA, NEW SPECIES, THE NONPARASITIC DERIVATIVE OF THE PACIFIC LAMPREY

CARL L. HUBBS

ABSTRACT.—The Pacific lamprey, *Lampetra (Entosphenus) tridentata*, is now shown to agree with most parasitic species of the Petromyzoniformes in having evolved into a nonparasitic derivative, *L. (E.) lethophaga*. Although the parasitic form ranges widely, from central Baja California around the North Pacific periphery to southern Japan, varying greatly in adult size, the dwarfed nonparasitic form seems to be confined to the contiguous drainage basins of the Pit River (a Sacramento River headwater) in northeastern California, both above and below the Pit River Falls, and to the upper Klamath River system in south-central Oregon. These two drainage basins harbor additional endemic fishes, and have certain other faunal features in common. The distributions of the three nonparasitic lampreys in the drainage basins around the North Pacific appear to be complementary.

L. lethophaga contrasts rather sharply with the dwarfed, probably resident types of *L. tridentata* in the Klamath system, as well as with the large, sea-run populations. However, a specimen from Willow Creek in the Lost River system of Oregon is possibly intermediate between *L. lethophaga* and the dwarf parasitic types in the Klamath River system; and a parasitic form of the same group, of Miller Lake, in a disjunct section of the Klamath River system, is reported to be even more dwarfed than *L. lethophaga*. Some intergradation between the parasitic and nonparasitic stocks is not excluded.

The dentition of the nonparasitic form exhibits features both of reduction and of increased individual variation, probably along with some geographical differentiation.

Like other lampreys, the new species no doubt exists for several years in the larval (ammocete) stage before metamorphosing in the autumn. The gonads ripen as the gut atrophies. The dwarf adults after overwintering appear on circumstantial evidence either (1) to undergo the typical nuptial metamorphosis to spawn in the following spring, or (2) to attain maturity neotenually while retaining the prenuptial state of pigmentation and body form, and to spawn over the summer months, or even after overwintering again.

There are indications that lamprey species are subject to regional diversity, and that some of the speciation has been of a mosaic type.

RESUMEN.—Se demuestra que la lamprea del Pacífico, *Lampetra (Entosphenus) tridentata* concuerda en su evolución con la mayor parte de las especies parasíticas de Petromyzoniformes, produciendo un derivado no parasítico, *L. (E.) lethophaga*. Las formas parasíticas presentan una amplia distribución geográfica, extendiéndose a lo largo de la zona periférica del Pacífico Norte, desde la parte central de Baja California hasta la zona meridional del Japón. Los adultos de estas formas ofrecen una gran variación de tallas. Las formas enanas libres, no parasíticas, están al parecer confinadas a las cuencas fluviales contiguas del río Pit (uno de los tributarios de la parte alta del río Sacramento) en la zona nordeste de California, a ambos lados de las cataratas del río Pit, y en la parte alta del sistema del río Klamath en la zona centro-meridional de Oregon. Estas dos cuencas fluviales albergan también otros peces endémicos, presentando así mismo otras características faunísticas comunes. Las tres lampreas no parasíticas que habitan las cuencas fluviales que bordean el Pacífico Norte, presentan al parecer una distribución complementaria.

L. lethophaga contrasta notablemente con las formas enanas, probablemente tipos residentes de *L. tridentata* en la red fluvial del Klamath, así como también con las especies de talla grande correspondientes a poblaciones oceánicas. Sin embargo, un ejemplar procedente de Willow Creek, en la red fluvial del río Lost, en Oregon, es posiblemente una forma intermedia entre *L. lethophaga* y los tipos parasíticos y enanos del sistema del río Klamath. Una forma parasítica de este mismo grupo aparece en el lago Miller (sección disyuntiva de la red fluvial del río Klamath). Se ha establecido ya, que dicha forma es aun más pequeña que *L. lethophaga*. Desde luego no puede excluirse la posibilidad de que exista una intergraduación entre las poblaciones parasíticas y libres (no parasíticas).

Las formas libres presentan variaciones individuales de reducción o de incremento en la dentición, características probablemente relacionadas con otras diferencias geográficas.

Al igual que sucede en otras lampreas, esta nueva especie permanece indudablemente durante varios años en la fase larval (amoceto) antes de llegar a la metamorfosis, que tiene lugar en el otoño. Al madurar las gónadas, el tubo digestivo se atrofia. Los adultos enanos después de pasar el invierno, evidencian cualquiera de las siguientes circunstancias: 1) que pasan la metamorfosis nupcial típica para así desovar en la primavera siguiente, o 2) alcanzan una madurez neoténica, es decir, retienen la pigmentación y forma del cuerpo de la fase prenupcial, desovando entonces durante los meses de verano, o aún más tarde, después de pasado el invierno.

Las observaciones obtenidas indican que las especies de lampreas presentan diversidad regional, y en algunos casos la especiación corresponde al tipo de mosaico.

Although I discovered a dwarfed, nonparasitic derivative of the Pacific lamprey, *Lampetra (Entosphenus) tridentata* (Richardson) in 1934, in the Pit River system of northern California and in the upper Klamath River system in southern Oregon, and although it has been distinguished by Bond (1961: 14) in key form from *L. tridentata*, from the same river systems, it has not yet been assigned a species-group name. Bond merely designated it "Klamath brook lamprey, *Lampetra* sp." With the particular need of making the name and the status of this form available for a forthcoming treatment of the distribution, phylogeny, and taxonomy of lampreys (Hubbs and Potter, in press), it is now belatedly made known as:

PIT-KLAMATH BROOK LAMPREY

Lampetra (Entosphenus) lethophaga, new species

Entosphenus tridentatus (misidentification).— Rutter, 1908: 120 (material listed from "South Fork Pitt River" only).

Lampetra planeri (misidentification).— Hubbs, 1925: 594 (size of recently transformed specimen from "North Fork of Pitt River").

Lampetra sp.— Bond, 1961: 14 ("Klamath brook lamprey"; "Klamath and Pit River systems").

Holotype, U. Mich. Mus. Zool. 130648, and paratypes, UMMZ 130649, from source of Fall River, a tributary to Pit River, in Shasta County, California (as specified under Location 2, below).

This species is illustrated in Figures 1, 2 A-B, and 6; its range and habitat in Figures 3 and 4; its size in Figure 8. Figures 2 C-D, 3, 5, 7, and 8 pertain in part or *in toto* to related forms.

Diagnosis.— The following diagnosis largely follows the sequence of characters utilized by Hubbs and Potter (in press) in their analysis of the lampreys of the world.

A petromyzonid lamprey agreeing with *Lampetra (sensu lato)* in having: the extraoral teeth not in regular alate rows, the lateral and posterior fields of disc essentially toothless between circumorals and marginals, the teeth of the anterior field few and scattered, none of the teeth villiform, the supraoral markedly dilated, the anterior circumorals normally 5, the total anterior and lateral circumorals usually 13, and the lateral circumorals more or less dilated. Agreeing with subgenera *Lethenteron* and *Entosphenus* in having the laterals connected by the posterior circumorals, and agreeing with *Entosphenus* in having 4 lateral circumorals on each side, one or more outer posterior circumorals often bifid, the supraoral often with a median cusp, the transverse lingual lamina almost rectilinear and with median cusp not strongly enlarged, and the marginals and posterior circumorals often in an irregular file. Differing from the complex now passing as *Lampetra tridentata* in being nonparasitic (not feeding or growing after the fall metamorphosis, but developing the gonads as the gut atrophies prior to spawning in the next spring or summer, or even later, and then dying), and in being much reduced in size at maturity (less than 170 mm), and in some places (including the type locality) breeding in prenuptial coloration and body form;